Behavior Genetics, Vol. 34, No. 6, November 2004 (© 2004)

A Genetic Analysis of Avian Personality Traits: Correlated, Response to Artificial Selection

Kees van Oers,[1,2,3] Gerdien de Jong,[2] Piet J. Drent,[1] and Arie J. van Noordwijk[1]

Received 14 Aug. 2003—Accepted 17 June 2004

Individuals in a range of species consistently differ in their behavior towards mild challenges, over age and time. Differences have been found for several personality traits in a range of species. In great tits these traits have a genetic basis and are phenotypically correlated. Estimates of genetic correlations are, however, fundamental to understanding the evolution of consistent individual differences in behavior. This study analyzed two selection experiments on two avian personality traits, early exploratory behavior and risk-taking behavior. The selection lines used were both started using wild great tits (*Parus* major) from two natural populations. Genetic correlations were calculated using the response and the correlated response to artificial selection. We found genetic correlations ranging from 0.51 to 0.66, based on individual values, and from 0.84 to 1.00 based on nest means. Genetic correlations can be due to pleiotropic effects or to linkage disequilibrium. The different behavioral traits might therefore have a common genetic basis, possibly constraining independent evolution of personality traits in natural populations. These results are discussed in relation to domain generality and domain specificity of personalities.

KEY WORDS: boldness; exploration; genetic correlation; *Parus major*; personalities; risk-taking behavior.

INTRODUCTION

Individuals within populations of many animal species differ in their behavioral reaction towards novel challenges (Gosling and John, 1999; Wilson *et al*., 1994). These differences between individuals in a range of correlated behavioral or physiological traits are consistent over age and context, and have been labeled as temperament, coping strategies, styles or syndromes (Boissy, 1995; Koolhaas *et al*., 1999; Wechsler, 1995), often comparable to human personalities (Eysenck and Eysenck, 1985; John, 1990; Zuckerman, 1991). Evidence is accumulating that the personality concept not only exists in humans, but also in other animal species (Clarke and Boinski, 1995; Gosling, 2001; Gosling and Vazire, 2002; Wilson *et al*., 1994). Two conditions have to be fulfilled for separate personality traits to represent a syndrome. First, the behavioral traits must be heritable. Secondly, the behavioral traits have to be correlated within a single context. Phenotypic correlations between behavioral traits have been reported for several domesticated and wild species (see Sih *et al*., 2003). In contrast, other studies found low phenotypic correlations between personality traits and subscribed this to context specificity (Coleman and Wilson, 1998; Réale *et al*., 2000). The evolution of quantitative characters, however, depends on genetic variation and genetic correlations. A genetic background for personality traits is generally accepted, but studies on the genetic structure of personality traits in natural

[1] Department of Population Biology of Animals, Netherlands Institute of Ecology, P.O. Box 40, 6666 ZG, Heteren, The Netherlands.

[2] Evolutionary Population Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands.

[3] To whom correspondence should be addressed at Department of Population Biology of Animals, Netherlands Institute of Ecology, P.O. Box 40, 6666 ZG Heteren, The Netherlands. Fax: +31-26-4723227. e-mail: k.vanoers@nioo.knaw.nl

0001-8244/04/1100-0611/0 © 2004 Springer Science+Business Media, Inc.

populations are missing. The genetic structure, however, both determines the course of selection and is itself determined by selection on trait combinations.

Genetic correlations between traits might constrain evolutionary change of either of these traits, since during selection genetic correlations influence the selection response. In a natural population, genetic correlations might provide information on past selection for combinations of particular traits (Lande and Arnold, 1983; Maynard Smith *et al.*, 1985). Two possible mechanisms may be responsible for genetic correlations. First, in the case of pleiotropy, individual genes have effects on several traits. Second, traits can be affected by different sets of genes, but a selective force, which generates and preserves particular combinations of alleles at a particular locus, causes linkage disequilibrium (Falconer and Mackay, 1996; Lynch and Walsh, 1998; Price and Langen, 1992).

In great tits, exploratory behavior (Verbeek *et al.*, 1994) is phenotypically correlated with aggression (Verbeek *et al.*, 1996), foraging behavior (Drent and Marchetti, 1999; Marchetti and Drent, 2000), the physiological reaction to stress (Carere *et al.*, 2001) and with risk-taking behavior (van Oers *et al.*, 2004a). An "early exploratory behavior" score was developed on the combination of two tests, reaction to a novel environment and reaction to a novel object. A four-generation, bi-directional selection experiment on early exploratory behavior (Drent *et al.*, 2003) showed that it had a genetic basis, and van Oers *et al.* (2004a) repeated this selection experiment on risk-taking behavior. In a study on wild great tits that were tested for exploration in the laboratory, individuals also differed consistently in exploration behavior and a comparable heritability was found through parent–offspring regression (Dingemanse *et al.*, 2002). Besides additive genetic variation, van Oers *et al.* (2004b) showed that exploration has a substantial nonadditive component. These consistent, heritable and co-varying reactions toward novel challenges add weight to the concept of the existence of avian personalities.

The existence of several avian personality traits that are phenotypically correlated and have an additive genetic component give scope to the co-evolution of different traits. Genetic correlations which could measure this are, however, difficult to estimate in natural populations, since they require large datasets on individuals with known pedigrees (Cheverud, 1988). We have therefore used a traditional quantitative genetic method to calculate genetic correlations here, based on data of two bi-directional selection experiments concerned with early exploratory behavior and risk-taking behavior. These two behaviors are proposed to represent personality traits (van Oers *et al.*, 2004a), comparable to Novelty seeking and Harm avoidance in the Three-dimensional Personality Questionnaire (TPQ), used in human personality research (Eysenck and Eysenck, 1985). We subsequently consider existing ideas on the functional structure of personalities and the domain specificity of personality traits, and compare our genetic correlations with previously found phenotypic correlations, to see if phenotypic correlations between these traits are similar to estimates of genetic correlations. Finally, we place our results in a broader framework, discussing the evolution of adaptive behavioral traits in natural populations.

METHODS

Exploration of A Novel Environment

We recorded exploration of a novel environment (analogous to an open field test; Walsh and Cummins, 1976) 1 day after birds had been housed individually at an age of 30–35 days. Observations were made between 0815 and 1230 h. Birds were deprived of food at least 2 h before testing. The test was conducted in an observation room of $4.2 \times 2.5 \times 2.3$ m containing five artificial trees (for a schematic overview of the room see Dingemanse *et al.*, 2002). Eight sliding doors along each 4.2 m wall connected the birds' living cages with the observation room. The birds went into the observation room and back without handling, by darkening the cages or the room.

As a measure of exploratory behavior we used the time to reach the fourth out of five trees, and converted this time into a linear score, where a score of 10 was given to birds that reached the fourth tree within one minute after landing on the first tree. Birds that did not visit four different trees within 10 minutes were given a score of 0.

Reaction Toward A Novel Object

Observations of reactions toward novel objects were made 10 and 12 days after the novel environment test. Tests were conducted in standard cages of $0.9 \times 0.4 \times 0.5$ m with solid bottom, top, side and rear-walls, a wire-mesh front and three perches. Birds were kept under natural light condi-

tions and had acoustical and visual contact with other lighted individuals. A curtain with a view hole separated the observer from the cage. For the tests a ''novel object'' was introduced on one of the outer perches. For this, a penlight battery was used for the first test and an 8 cm bendable Pink Panther toy for the second test. A score ranging from 0 to 5 was given by means of a combination between the latency to approach the object, and the shortest distance to the object. The maximal score of 5 was given to birds that pecked the object, and a score of 0 was given to birds that did not visit the perch on which the object was placed within 120 seconds.

Early Exploratory Behavior

To measure early exploratory behavior a novel environment test was followed by two tests of reaction to novel objects. The combination of the score of the novel environment test and the scores of the novel object tests is referred to as early exploratory behavior.

Risk-Taking Behavior

This test measured the latency to restart foraging after a startle. We placed three artificial trees and a feeding table with a bowl of mealworms in the observation room described above (for a schematic overview of the setup see van Oers *et al.*, 2004a). The feeding table was equipped with a spring loaded, hinged steel plate to startle the bird. A cord that was connected to this plate was led through the keyhole of the door, so that the observer could handle it from outside the observation room: releasing the pressure on the cord caused the plate to immediately spring up in front of the bird and pulling the cord back brought the plate to its original position. Birds entered the room as described in the novel environment test, landed on a tree and after a while visited the feeding table to take a mealworm, which they ate while sitting on an artificial tree. Upon returning to the feeding table with the intention to take a second worm, they were startled just before they were able to take it. After the startle we measured the time to return to the feeding table and actually take their second worm: termed the startle latency (for more details on the startle test see van Oers *et al.*, 2004a). The startle latency test took place 6–8 weeks after the novel object tests (90–100 days after hatching).

Bi-Directional Artificial Selection Experiments

Early exploratory behavior was used as the selection criterion in the bi-directional selection experiment of Drent *et al.* (2003). In total, 79 nestlings of 11 nests were used for the analyses on the parental generation. In the fourth generation of selection, we had 14 nests with 38 individuals of the high line and 9 nests with 35 birds of the low line available for analysis.

The startle latency was used as selection criterion for the bi-directional selection on risk-taking behavior (van Oers *et al.*, 2004a). In the second generation, data was available for 7 nests of the high line (38 individuals) and 8 nests of the low line (35 individuals).

Both selection procedures were similar, and details of pair/formation, incubation, cross-fostering and hand rearing are described by Drent *et al.* (2003).

Genetic Correlations

The genetic correlations were calculated using the response and the correlated response to artificial selection using the formula (Falconer and Mackay, 1996: pp. 316–318):

$$r_A = \sqrt{[(CR_A/R_A) \times (CR_B/R_B)]}, \qquad (1)$$

where CR_A is the correlated response of behavior A to the artificial selection on behavior B, CR_B is the correlated response of behavior B to the artificial selection on behavior A. R_A and R_B are the responses to artificial selection of behavior A and behavior B, respectively. Genetic correlations were calculated for risk-taking behavior *versus* early exploratory behavior, as well as for risk-taking behavior *versus* the novel environment and novel object test behaviors, separately.

To obtain a measure of confidence, two different types of estimates of each of the three genetic correlations were calculated. For the first type of estimate, the response and correlated response were calculated as the difference between the high and low lines of the selection line experiments. For the second type of estimate, the responses of each of the selection line experiments were split into two parts: The difference between the mean of the high lines and the mean of the original parental generation (high) and the difference between the mean of the low lines and the mean of the parental

generation (low). This creates four possible combinations to calculate genetic correlations (high–high, high–low, low–high, low–low = 4 (estimates). These estimates are not independent measures of the genetic correlations and are therefore not used to assess the variation in genetic correlations. Genetic correlations were calculated using both individual values and nest means.

Statistical Analyses

Because the variance in startle latency time increased with the mean value, this variable was log transformed (Zar, 1999) for all analyses with normal distributions. To control for between-year variation we used 250 birds raised during the selection experiment as a control population by subtracting the mean value of the control group from the individual values. None of these control birds were part of either selection experiment. All tests were based on nest means, unless stated otherwise. We used *t*-tests to compare line means. The estimation of the power and the required minimal sample size for a power of 80% of these tests was done with a power test (Zar, 1999: pp. 134–136). All statistical tests are two-tailed, and *p*-values ≤ 0.05 are considered as being significant. We used SPSS version 10.1 for Windows for all analyses.

RESULTS

The responses and correlated responses to selection, corrected for the number of generations, are given in Figure 1. Based on the analysis of nest means, the lines selected for early exploratory behavior, significantly differed in their correlated response of risk-taking behavior (Table I). The lines selected for risk-taking behavior significantly differed in novel environment behavior, but not in novel object behavior and early exploratory behavior (Table I). The absence of a significant difference between the lines for reaction towards a novel object and early exploratory behavior is most likely caused by a lack of power due to a small sample size, since the lines differed in their correlated responses in the same manner for all traits. This is confirmed in a power analysis and when the minimal adequate sample sizes were calculated (Table I). Therefore we may conclude that "fast" explorers have shorter startle latencies than "slow" explorers and "high" risk-takers explore a novel room more quickly and approach a novel object more easily than "low" risk takers do.

Genetic correlations calculated on individual scores range from 0.51 to 0.66 (Table II). Genetic correlations calculated from nest means range from 0.84 to 1.00 (Table III). The correlation between risk-taking behavior and early exploratory behavior (*t*-test; $t_5 = -1.53$ and $p = 0.20$) and between risk-taking behavior and boldness (*t*-test; $t_5 = -2.01$ and $p = 0.12$), calculated using individual scores did not differ from the correlation calculated from nest means. The correlations between risk-taking behavior and exploration did differ (*t*-test; $t_5 = -2.89$ and $p = 0.045$) between the two methods.

DISCUSSION

We demonstrate that avian personality traits are genetically correlated and present genetic correlations ranging from 0.51 to 0.66 for individual test values and from 0.84 to 1.00 based on nest means. These results indicate that natural selection on one trait has consequences for the correlational selection on other traits. Either shared genes or strong correlated selection can be the cause of these high genetic correlations.

The five different estimates of the genetic correlations are not independent measures of the genetic correlation between the avian personality traits. These give no information about the variation in genetic correlations, but we use them purely to get a measure of confidence for our methodology.

A possible concern in our experimental setup is the lack of control and replicate lines in our selection experiments (see e.g., Henderson, 1989). Since setting up selection lines for a long living wild animal like the great tit has its limitations, we chose to enlarge our sample size per generation rather than incorporate a control line. To be able to study genetic correlations we chose to select for startle latency rather than repeat the first selection experiment. Although responses were found in both selection lines, studies have shown that correlated responses could not have been as straightforward as presented (Gromko, 1995). Experimental testing of the agreement between responses and correlated responses has shown ambiguous results (see Gromko *et al.*, 1991). Our study, however, is in line with other studies where selection on a trait produced the expected, positively correlated responses in another trait (see Gromko *et al.*, 1991).

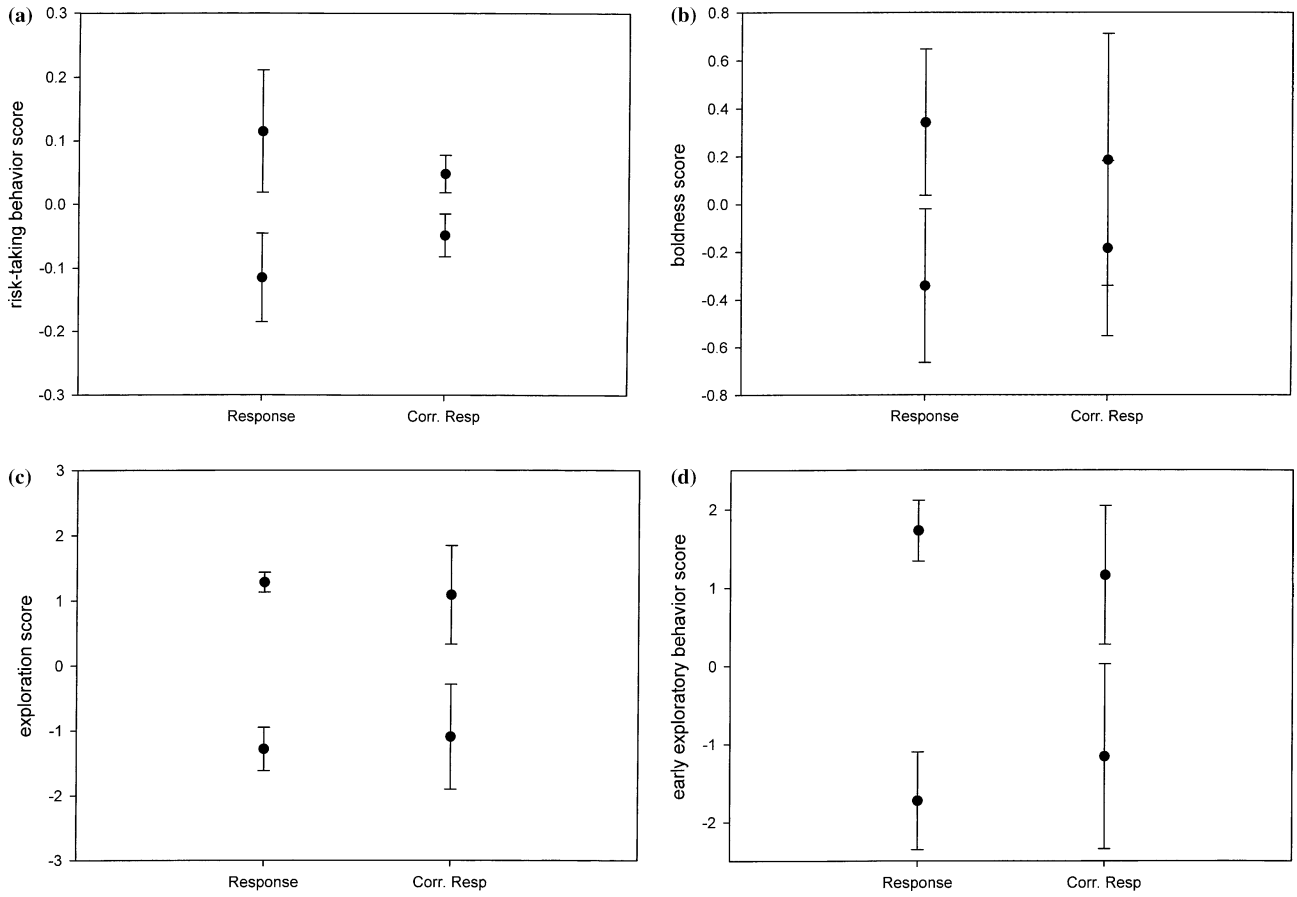

Fig. 1. Response and correlated responses to artificial selection. Values are corrected for year effects and scaled toward one. Figures represent (a) response of *risk-taking behavior* to selection on risk-taking behavior and its correlated response to the selection on early exploratory behavior, (b) response of *boldness* to selection on early exploratory behavior and its correlated response to selection on risk-taking behavior, (c) response of *exploration* to selection on early exploratory behavior and its correlated response to selection on risk-taking behavior and (d) response of *early exploratory behavior* to selection on early exploratory behavior and its correlated response to selection on risk-taking behavior. Mean values calculated on individual scores are given together with their standard errors.

Table I. Correlated Responses for the Selection Experiments on Risk-Taking Behavior (RTB) and Early Exploratory Behavior (EEB)

	Correlated Response							
Trait	High Line	*n*	Low Line	*n*	*t*	*p*	Power	M.A.S.
RTB	-0.259 ± 0.081	14	0.064 ± 0.092	9	-2.570	0.02	74.8%	10
EEB	-0.749 ± 1.162	8	1.584 ± 1.150	7	-1.427	0.18	29.7%	21
Exploration	-1.112 ± 0.553	7	1.281 ± 0.896	7	-2.273	0.04	62.3%	8
Boldness	-0.428 ± 0.605	7	0.375 ± 0.780	7	-0.825	0.42	12.9%	69

Correlated responses ($\pm$ standard error) are given for the high and low lines separately. n = number of nests, power = power of test given

The genetic correlation between risk-taking behavior and novel object behavior was close to one, and higher than the correlation between risk-taking and novel environment behavior. This suggests that the same genes are involved in the reaction towards a novel object and the response to a possible risk (i.e. a predator). This is an interesting finding since reaction towards a novel object is, in animal research, often taken as a measurement for the propensity to take risks (e.g. Coleman

Table II. Genetic Correlations and their Standard Errors Between Risk-Taking Behavior (RTB) and Early Exploratory Behavior (EEB), Exploration and Boldness

Traits	r_A	t	p
RTB and EEB	0.58 ± 0.25	2.30	0.08
RTB and Exploration	0.51 ± 0.15	3.46	0.03
RTB and Boldness	0.66 ± 0.34	1.96	0.12

Table III. Genetic Correlations and their Standard Errors between Risk-Taking Behavior (RTB) and Early Exploratory Behavior (EEB), Exploration and Boldness

Trait	r_A	t	p
RTB and EEB	0.84 ± 0.27	3.11	0.04
RTB and Exploration	1.00 ± 0.32	3.15	0.03
RTB and Boldness	0.94 ± 0.29	3.26	0.03

and Wilson, 1998), whereas, in human personality research risk-taking behavior is seen as a separate domain (Eysenck and Eysenck, 1985). The high correlation between risk-taking and novel environment behavior indicates that the two traits have many genes in common but are not completely identical. It could therefore well be that the traits are not independent traits, but different measurements of the expression of the same group of genes. Differences between the genetic correlations are then a result of sampling errors. Genetic correlations have high standard errors, which become evident in repeated selection experiments, since each sample from a natural population just contains a sampling of the polymorphic pleiotropic loci that cause the genetic correlation (Gromko, 1995). In each sample some of the genes may be lacking variation just by chance. A second reason for sampling errors can be the sample size. In a review, Cheverud (1988) studied the difference in correlation level between phenotypic and genetic correlations. He showed that the discrepancy between the two estimates decreases with increasing effective sample size. Since we are aware of the relatively low effective sample sizes in our study, this has to be taken into account.

Domain Specificity Versus Domain Generality

In studies on animal personalities two different approaches can be ascertained. One approach makes use of factorial analysis as used in human personality studies and describes the same main dimensions with, in addition, two extra dimensions (for a review see Gosling and John, 1999). The other part of the research on consistent individual differences in animals is based on studies of single traits (Armitage, 1986; Benus *et al.*, 1987; Benus, 2001; Réale *et al.*, 2000; Sluyter *et al.*, 1996; Wilson *et al.*, 1993). In studies on coping styles or strategies, mostly on domesticated animals, these behavioral traits are linked to physiological parameters (Koolhaas *et al.*, 1999). These different approaches find both genetic and environmental influences on the traits but a general question within each of these approaches is whether these traits are domain general or domain specific (Wilson et al., 1994). Domain specificity, or context dependence, is most often linked to the presence of phenotypic correlations of one trait measured in multiple contexts (Réale *et al.*, 2000; Sih *et al.*, 2003; van der Kooij *et al.*, 2002; van Oers, 2003; Wilson, 1998).

Since the behavioral traits studied are measurements of reactions to an external stimulus, variation in behavior between contexts can be dependent on several factors. In addition to the effect of the context itself, learning effects, variation in the stimulus or measurement variation can be responsible for the lack of phenotypic correlation between traits in multiple contexts.

In our results, genetic correlations are higher when we control for within-nest variance. Since only special environmental effects influence genetic correlations, we can expect that general environmental effects are not responsible for this difference between the genetic and phenotypic correlations. This is confirmed by our earlier studies, where repeatability estimates of early exploratory behavior and risk-taking behavior were not higher than our heritability estimates (Dingemanse *et al.*, 2002; Drent *et al.*, 2003; van Oers *et al.*, 2004a).

Pleiotropy Versus Linkage Disequilibrium

The functional architecture of personality traits has been debated in various approaches to personality research. All approaches on consistent individual differences in behavioral traits have in common that they report an underlying genetic structure that causes the coherence of these traits, either due to pleiotropic effects (multiple effects of individual genes) or to linkage disequilibrium (nonrandom

association between alleles at different loci) (Bouchard and Loehlin, 2001).

A general set of pleiotropic genes could be the basis for differences in personalities, but some exclusive genes additionally influence each separate personality trait. Elliot and Thrash (2002) stated that approach–avoidance motivation might be seen as such a unifying thread of personality, since it forms the foundation of several of the main traits as used in human psychology. In the studies of coping styles in rodents where a more physiological approach is used to study consistent individual differences, personalities are believed to be rooted in a genetically based differential use of physiological mechanisms (Koolhaas *et al*., 1999).

Consistent individual differences are generally accepted to be adaptive (Buss and Greiling, 1999; Wilson, 1998), and evolution is responsible for numerous solutions to problems, rather than one adaptive mean surrounded by nonadaptive variation. The coherence between different personality traits could therefore also be a product of natural selection. Even if the separate traits are inherited due to independent sets of loci but interactively affect fitness, linkage disequilibria may build up through correlated selection (Lande and Arnold, 1983), which is referred to as fitness epistasis (Whitlock *et al*., 1995). Selection against particular combinations of traits cause other combinations to be more frequent. However, unless correlational selection is strong and chronic (Sinervo and Svensson, 2002), linkage disequilibria which are enhanced by correlational selection may be expected to rapidly dissipate (Falconer and Mackay, 1996).

When looking at our great tit system, it is likely that different personality traits share a greater part of their genes. The large genetic correlations of this study are one indication for this. A second indication was found by Dingemanse *et al*. (2004), who showed differences in selection pressures for males and females and different selection pressures over three different years, in a study on exploration in a natural population. Considering this together with the prerequisites of correlational selection, genetic correlations found in our study will be built up and maintained by correlated selection alone if variation in natural selection on one trait covaries with selection on another trait. As we expect this to be unlikely, we do not expect that our results can be explained by correlational selection alone.

CONCLUSION

The genetic correlations found in this study are high, most likely caused by pleiotropic effects, but linkage disequilibrium due to correlated selection cannot be completely ruled out. The discrepancy between the genetic correlations of this study and the phenotypic correlations of earlier studies is caused by special environmental effects. Our results do not support suggestions from other studies that correlated behaviors can be split up into two or more distinct axes, which are supposed to be under independent control through for example separate sets of genes (Budaev and Zhuikov, 1998; Elliot and Thrash, 2002; Wilson *et al*., 1994). More likely, selection on several correlated personality traits shape the form of any of the traits. Studying single behaviors will therefore only make sense when the results are considered in the context of the whole phenotype (Price and Langen, 1992).

ACKNOWLEDGEMENTS

We thank Piet de Goede, Niels Dingemanse, Margreet Klunder, Kathelijn de Maeijer, Chiara Marchetti, Ester van der Meer and Vera Ros for their assistance in bird collection and testing. We are grateful to Bart van IJmeren, Tanja Thomas, Mary-Lou Aaldering and Janneke Venhorst for care taking of the adult birds and assistance in hand rearing. Wil Keultjes built a great part of the experimental set-up. Denis Réale, Christiaan Both, and Erik Postma helped with earlier versions of the manuscript. Many students and volunteers helped with hand rearing of the birds, but we would especially like to thank Peet Jongerd, who developed and did a great deal of the hand rearing. Permission for animal collection, breeding, testing and blood sampling was granted to KO by the legal comity "KNAW Dier Experimenten Commissie" (DEC). KvO is supported by the Life Sciences Foundation (ALW grant 805-33-323). This is publication number 3300 of the Netherlands Institute of Ecology.

REFERENCES

Armitage, K. B. (1986). Individuality, social behaviour, and reproductive success in yellow-bellied marmots. *Ecology* **67**:1186–1193.

Benus, R. F. (2001). Coping in female mice from lines bidirectionally selected for male aggression. *Behaviour* **138**:997–1008.

Benus, R. F., Koolhaas, J. M., and van Oortmerssen, G. A. (1987). Individual differences in behavioural reaction to a changing environment in mice and rats. *Behaviour* **100**:105–122.

Boissy, A. (1995). Fear and fearfulness in animals. *Q. Rev. Bio.* **70**:165–191.

Bouchard, T. J., and Loehlin, J. C. (2001). Genes, evolution, and personality. *Behav. Genet.* **31**:243–273.

Budaev, S. V., and Zhuikov, A. Y. (1998). Avoidance learning and "personality" in the Guppy (*Poecilia reticulata*). *Comp. Psych.* **112**:92–94.

Buss, D. M., and Greiling, H. (1999). Adaptive individual differences. *J. Pers.* **67**:209–243.

Carere, C., Welink, D., Drent, P. J., Koolhaas, J. M., and Groothuis, T. G. G. (2001). Effect of social defeat in a territorial bird (*Parus major*) selected for different coping styles. *Physiol. Behav.* **73**:427–433.

Cheverud, J. M. (1988). A comparison of genetic and phenotypic correlations. *Evolution* **42**:958–968.

Clarke, A. S., and Boinski, S. (1995). Temperament in nonhuman-primates. *Am. J. Primatol.* **37**:103–125.

Coleman, K., and Wilson, D. S. (1998). Shyness and boldness in pumpkinseed sunfish: individual differences are context specific. *Anim. Behav.* **56**:927–936.

Dingemanse, N. J., Both, C., Drent, P. J., and Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proc. Roy. Soc. Lond. B.* **271**:847–852.

Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K., and van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory behaviour in wild great tits. *Anim. Behav.* **64**:929–937.

Drent, P. J., and Marchetti, C. (1999). Individuality, exploration and foraging in hand raised juvenile great tits. In N. J. Adams and R. H. Slotow (eds.), *Proceedings of the 22nd International Ornithological Congress*. Durban, Johannesburg: Birdlife South Africa.

Drent, P. J., van Oers, K., and van Noordwijk, A. J. (2003). Realized heritability of personalities in the great tit (*Parus major*). *Proc. R. Soc. Lond. B.* **270**:45–51.

Elliot, A. J., and Thrash, T. M. (2002). Approach–Avoidance Motivation in Personality:Approach and Avoidance Temperaments and Goals. *J. Pers. Soc. Psychol.*. **82**:804–818.

Eysenck, H. J., and Eysenck, M. W. (1985). *Personality and individual differences*. New York: Plenum.

Falconer, D. S., and Mackay, T. F. C. (1996). *Introduction to quantitative genetics*. New York: Longman.

Gosling, S. D. (2001). From mice to men: what can we learn about personality from animal research? *Psychol. Bull.* **127**:45–86.

Gosling, S. D., and John, O. P. (1999). Personality dimensions in nonhuman animals: a cross-species review. *Curr. Direct. Psychol. Sci.* **8**:69–75.

Gosling, S. D., and Vazire, S. (2002). Are we barking up the right tree? Evaluating a comparative approach to personality. *J. Res. Pers.* **36**:607–614.

Gromko, M. H. (1995). Unpredictability of correlated response to selection: pleiotropy and sampling interact. *Evolution* **49**:685–693.

Gromko, M. H., Briot, A., Jensen, S. C., and Fukui, H. H. (1991). Selection on copulation duration in *Drosophila melanogaster*: predictability of direct-response vs. unpredictability of correlated response. *Evolution* **45**:69–81.

Henderson, N. D. (1989). Interpreting studies that compare high-selected and low-selected lines on new characters. *Behav. Genet.* **19**:473–502.

John, O. P. (1990). The "big-five" factor taxonomy: dimensions of personality in the natural language abd in questionnaires. In L. A. Pervin (ed.), *Handbook of personality:theory and research*. New York: Guilford Press.

Koolhaas, J. M., Korte, S. M., De Boer, S. F., der Vegt, B. J., van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. W., and Blokhuis, H. J. (1999). Coping styles in animals: current status in behavior and stress-physiology. *Neurosci. Biobehav. Rev.* **23**:925–935.

Lande, R., and Arnold, S. J. (1983). The measurement of selection on correlated characters. *Evolution* **37**:1210–1226.

Lynch, M., and Walsh, B. (1998). *Genetics and analysis of quantitative traits*. Sunderland, MA:Sinauer Associates, Inc.

Marchetti, C., and Drent, P. J. (2000). Individual differences in the use of social information in foraging by captive Great Tits. *Anim. Behav.* **60**:131–140.

Maynard Smith, J., Burian, R., Kaufmann, S., Alberch, P., Campbell, J., Goodwin, B., Lande, R., Rauf, D., and Wolpert, L. (1985). Developmental constraints and evolution. *Q. Rev. Biol.* **60**:265–287.

Price, T., and Langen, T. A. (1992). Evolution of correlated characters. *TREE* **7**:307–310.

Réale, D., Gallant, B. Y., Leblanc, M., and Festa-Bianchet, M. (2000). Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Anim. Behav.* **60**:589–597.

Sih, A., Kats, L. B., and Maurer, E. F. (2003). Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. *Anim. Behav.* **65**:29–44.

Sinervo, B., and Svensson, E. (2002). Correlational selection and the evolution of genomic architecture. *Heredity* **89**:329–338.

Sluyter, F., Korte, S. M., Bohus, B., and van Oortmerssen, G. A. (1996). Behavioral stress response of genetically selected aggressive and nonaggressive wild house mice in the shock-probe/defensive burying test. *Pharmacol. Biochem. Behav.* **54**:113–116.

van der Kooij, E. V., Kuijpers, A. H., Schrama, J. W., van Eerdenburg, F. J. C. M., Schouten, W. G. P., and Tielen, M. J. M. (2002). Can we predict behaviour in pigs? Searching for consistency in behaviour over time and across situations. *Appl. Anim. Behav. Sci.* **75**:293–305.

van Oers, K. (2003). On the genetics of avian personalities: mechanism and structure of behavioural strategies in the great tit (*Parus major*). Ph.D. Thesis, Utrecht:University Utrecht.

van Oers, K., Drent, P. J., and van Noordwijk, A. J. (2004a). Realized heritability and repeatability of risk taking behaviour in relation to avian personalities. *Proc. R. Soc. Lond. B.* **271**:65–73.

van Oers, K., Drent, P. J., De Jong, G., and van Noordwijk, A. J. (2004b). Additive and nonadditive genetic variation in avian personality traits. *Heredity*, in press.

Verbeek, M. E. M., Boon, A., and Drent, P. J. (1996). Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour* **133**:945–963.

Verbeek, M. E. M., Drent, P. J., and Wiepkema, P. R. (1994). Consistent individual differences in early exploratory behaviour of male great tits. *Anim. Behav.* **48**:1113–1121.

Walsh, R. N., and Cummins, R. A. (1976). The open-field test: a critical review. *Psychol. Bull.* **83**:482–504.

Wechsler, B. (1995). Coping and coping strategies: a behavioural view. *Appl. Anim. Behav. Sci.* **43**:123–134.

Whitlock, M. C., Phillips, P. C., Moore, F. B. G., and Tonsor, S. J. (1995). Multiple fitness peaks and epistasis. *Ann. Rev. Ecol. Systemat.* **26**:601–629.

Wilson, D. S. (1998). Adaptive individual differences within single populations. *Phil. Trans. R. Soc. Lond. B.* **353**:199–205.

Wilson, D. S., Clark, A. B., Coleman, K., and Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *TREE* **9**:442–446.

Wilson, D. S., Coleman, K., Clark, A. B., and Biederman, L. (1993). Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *J. Comp. Psychol.* **107**:250–260.

Zar, J. H. (1999). *Biostatistical analysis*. New Jersey: Prentice-Hall.

Zuckerman, M. (1991). Basic dimensions of personality. In Zuckerman, M. (ed.), *Psychobiology of personality*. Cambridge: Cambridge University Press.

Edited by Peter Driscoll